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Type studies in *Helvella* (*Pezizales*) 1

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Abstract — Sixteen type and some additional specimens representing fifteen species assigned to *Helvella* were studied with the aim of providing new data for their improved delimitation and recognition. Specimens were received on loan from DAOM, FH, H, K, MA, MICH, S and UPS. A synoptic key to the studied species is provided to contribute to a better understanding of the genus and the taxonomy of the morphospecies. Original descriptions are emended to include data on the anatomy of the apothecial excipulum and stipe layers, apothecium and stipe reactivity to Melzer's reagent, and ascospore ornamentation. Reasons are given for maintaining *H. subglabra, H. atra, H. griseoalba,* and *H. costifera* as independent taxa and for considering *Helvella hyperborea* a synonym of *H. costifera*. Previously imprecise descriptive terms are clarified.

Key words — *Ascomycota*, holotype, isotype, lectotype, revision

Introduction

The genus *Helvella* L. includes approximately 52 species (Kirk et al. 2008). Its distribution is basically north temperate, with only one tropical species recognized (Dissing 1979). Traditional taxonomy of the genus has been based mainly on ascoma shape and color and the presence or absence of projecting hyphae on the sterile surface (ectal excipulum) of the apothecium (Dissing 1966b, Weber 1972, Abbott & Currah 1997). Characters such as ascus development (aporhynchous or pleurorhynchous), ascospore shape and size, paraphysis color, and the presence of pigment in the apothecium ectal excipulum cells have proven to be of taxonomic value in some species (Weber 1972; Harmaja 1977b, 1979; Abbott & Currah 1997).

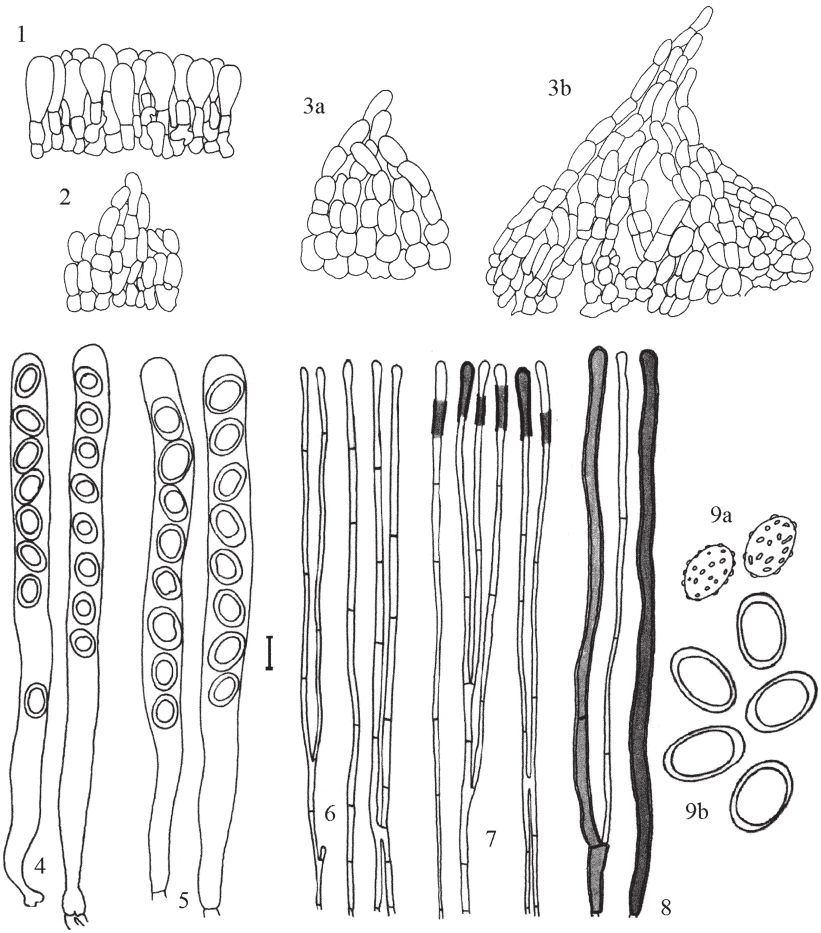
Although Nannfeldt (1937) proposed using the term "apothecium" specifically for *Helvella* to describe the entire ascoma, Weber (1972, 1975) and

Abbott & Currah (1988, 1997) used "apothecium" exclusively for the upper ascoma — i.e., the hymenium and its immediate supporting tissues — without the stipe. Eckblad (1968) commented that some authors carefully avoid the term apothecium for pileate forms like *Helvella*, whereas Dissing (1966b) and Calonge & Arroyo (1990) employed this term loosely, either for the complete ascoma or just for the upper part. Here, we follow Weber's (1972) concept, applying the term apothecium only for the upper ascoma, except that where she differentiated stipe tissues with "ectal excipulum" and "medullary excipulum," we use "outer layer" and "inner layer," because in discomycetes "excipulum" currently is interpreted as the "tissue or tissues containing the hymenium in an apothecium" (Kirk et al. 2008).

In all *Helvella* species the medullary excipulum and stipe inner layer are composed of "textura intricata" (interwoven hyphae) while the ectal excipulum and stipe outer layer are a "textura angularis" (almost isodiametric cells without intracellular spaces) (Korf 1952, Dissing 1966, Eckblad 1968, Weber 1972). These cells are arranged in rows perpendicular to the surface. In glabrous ascomata, the ectal excipulum external layer is a palisade of clavate hyphal end-cells, ending more or less at the same level (Fig. 1) (Weber 1972). Hairy ascomata have an ectal excipulum outer layer that Eckblad (1968) described as "consisting of more or less swollen chains of cells often converging into distinct clusters." These clusters are called "hyphal fascicles" (Weber 1972) or "chains of cells and/or fascicled hyphal chains" (Abbott & Currah 1997). Macroscopically, they give the appearance of pubescence or hairs of different lengths (Figs 2–3) and are important in the taxonomy of the genus (Dissing 1966). Descriptive terms used in the literature — "finely pubescent," "furfuraceous," "granulose," "hairy," "pruinose," "pubescent," "roughened," "velvety," "villose" (Dissing 1966; Weber 1972, 1975; Dennis 1981; Abbott & Currah 1997) — have generated confusion through their different meanings, incorrect application, and/or the lack of consistent usage. Kaushal (1991) alone consistently uses only "pubescent" to describe the hairs; furthermore he included the hyphal fascicle length for each species.

Only three papers have described the stipe tissue: Gómez & Herrera (1965) and Weber (1972, 1975). Gómez & Herrera concluded that because stipe tissue is continuous with apothecium tissue, it is not a useful character. Although Weber (1972) described both tissues as similar in color and structure, she did indicate color differences between tissues in some species descriptions.

Pigment distribution, mainly in ectal excipulum cells (see Figs 19–21) and paraphyses — i.e., intracellular (cytoplasmic), in the cell wall, or encrusting (deposited pigment forming an irregular crust on the wall) — is controversial. Eckblad (1968), Weber (1972), and Harmaja (1977b, 1979) considered pigmentation to be diagnostic. Eckblad (1968) wrote it is a characteristic mostly



Figs 1–9. 1: Ectal excipulum of a glabrous apothecium (*Helvella leucopus* var. *populina*). 2: Hyphal fascicle of the outer layer of a subpubescent stipe (*H. griseoalba*). 3: Hyphal fascicle of the ectal excipulum of a pubescent apothecium (*H. costifera*)—a: short, b: large. 4: Pleurorhynchous asci (*H. pocillum*). 5: Aporhynchous asci (*H. crassitunicata*); 6: Common paraphyses (*H. subglabra*). 7: Paraphyses with a thick-walled brown cap or collar at the apex (*H. paraphysitorquata*). 8: Thick-walled paraphyses (*H. crassitunicata*). 9: Ascospores (*H. solitaria*) —a: ornamented, b: smooth. Scale bars: 1–8 = 20 µm, 9 = 8 µm.

used on species level in *Pezizales*, but "[u]nfortunately too many descriptions simply state whether the paraphyses are coloured or not, not where the pigments are located." With respect to *Helvella*, Eckblad (1968) noted, "[c]hemically and genetically it is probably a very short step from pigmented paraphyses to

hyaline ones, e.g. from the greyish-black paraphyses of *Helvella lacunosa* to the colourless paraphyses of *H. crispa*." Weber (1972) recognized two patterns of pigment distribution: 1) intracellular pigments, occurring in species with buff, tan or brown ascomata, and 2) pigments associated with hyphal walls, characteristic of gray to black species. On the other hand, Dissing (1966b) and Abbott & Currah (1997) considered pigmentation as highly variable and of limited use in circumscribing *Helvella* species. Dissing (1966b) indicated it is difficult to assess, especially in species where hymenium color variation is very large (as in *H. lacunosa* Afzel.) and hymenium color ranges from pale gray to gray brown to black due to pigments in the paraphyses**.** Only Dissing (1964, 1966b) went beyond just describing the colors of the structures; he also evaluated the color before and after treatment with cotton blue. Unfortunately, no further works analyze this issue.

Chemical reactions to Melzer's reagent have not been considered as diagnostic characters for structures other than ascospores or asci. Although excipulum cells in other ascomycete genera (*Perrotia*, *Hymenoscyphus*, *Epibryon*) show a hemiamyloid reaction, its taxonomic value is uncertain (Baral 1987).

Helvella ascospores have limited taxonomic value. In fact, their size is a key feature only for *H. pocillum* and *H. crassitunicata* (Weber 1975; Harmaja 1976), while the fusoid to subfusoid shape (differing from the typically ellipsoid ascospores found elsewhere) is found only in *H. macropus* (Pers.) P. Karst. (Abbott & Currah 1997) and *H. terrestris* (Velen.) Landvik (Landvik et al. 1999). Ascospore ornamentation is highly complex and a subject of controversy. Dissing (1964) and Dissing & Nannfeldt (1966) regarded ornamented ascospores in *Helvella* as immature, while Weber felt (1972) that they corresponded to the mature condition. Eckblad (1968) described ascospores with "false ornamentation," and Schumacher (pers. com.) mentioned that during the final stage of ascospore development, some secondary wall remnants might adhere to the ascospore surface, producing a highly inconsistent pattern; typically, a number of ascospores do not get such adherences at all and consequently remain smooth. On the other hand, Abbott & Currah (1997) gave to this character a high value, because they considered verruculose ascospores unique to the subgenus *Macropodes* (Dissing) S.P. Abbott.

Species concepts are similarly varied. Some authors with a narrow species concept, such as Harmaja (1976, 1977a,b, 1979), segregated species based on subtle differences. Others with a wider species concept (e.g., Abbott & Currah 1997) use fewer diagnostic characters to separate *Helvella* species. The purpose of our study was to review selected *Helvella* type specimens to delimit morphospecies and to determine which characters could be used in taxonomic and phylogenetic studies of the genus. We present five sets of types belonging to species with problematic delimitations: 1) *H. costifera* vs. *H. hyperborea*

and *H. griseoalba*; 2) *H. crassitunicata* vs. *H. pocillum*; 3) *H. subglabra* vs. *H. atra*; 4) *H. solitaria* vs. *H. queletii* and *H. ulvinenii*; and 5) *H. verruculosa* vs. *H. dryadophila*. We also add to the earlier descriptions of *H. leucopus* var. *populina*, *H. maculata*, *H. paraphysitorquata*, and *H. robusta*. Finally, we suggest a set of standard terms to clarify descriptions of *Helvella* species.

Materials & methods

Sixteen type as well as some additional specimens from eight herbaria (DAOM, FH, H, MA, MICH, O, S, UPS) were studied. Herbarium abbreviations follow Holmgren et al. (1990). Free-hand sections from apothecium and stipe were made with a razor blade directly from dry specimens. Sections and mycelium were placed first in 70% ethyl alcohol and subsequently in water to rehydrate the tissues. Specimens were examined under a Zeiss Axioskop 2 plus microscope with a drawing tube. Microphotographs were taken under a Zeiss Axioskop 40 microscope using Axio Vision 4 software. Ascospore measurements were made on mature free spores outside the asci, or on those attached to the hymenial surface, stipe, or basal mycelia. Mounts from apothecium, stipe, and mycelium were also made in Melzer's reagent (without pre-treatment in KOH) and cotton blue. We follow in part the terminology used by Baral (1987) to describe the hemiamyloid reaction in Melzer's reagent ('Melzer's'): "rr+" for hemiamyloid ("solely red") reaction and "rr–" for negative reaction. All measurements and features recorded are from type specimens. Where additional non-type specimens were studied for some species, observations that differ from those of the type are indicated under "Remarks" but not included in the technical description.

Terms used to refer to the surface of the apothecial ectal excipulum and stipe outer layer are: GLABROUS (FIG. 1), SUB-PUBESCENT (for fascicled hyphal chains < 50 µm long; FIG. 2), and PUBESCENT (for fascicled hyphal chains > 50 µm long; FIG. 3). As the hairs' length can vary in the last case, their measurements are given in the descriptions. See also "Results & discussion".

Results & discussion

We studied sixteen type specimens and present only new information or data that differs from the protologue or previous publications. In addition to the characters established by previous authors (Dissing 1966b; Calonge & Arroyo 1990; Abbott & Currah 1997), we found that pigmentation of apothecial cells, stipe tissue anatomy, and the reddish (hemiamyloid) reaction in Melzer's reagent (FIGS 10–11) are important characters that contribute to species recognition in *Helvella*. Because we found no variation in the basal mycelium of the stipe, which is universally composed of smooth-walled, hyaline, rr–, interwoven hyphae, we do not include it in the species descriptions. Nor do we make further mention of the fact that ascospores of all species have both cyanophilic cytoplasm and ornamentation (when present).

Regarding the value of pigmentation in the structures, we think it is important to study it from two perspectives: a) location and b) intensity. Concerning

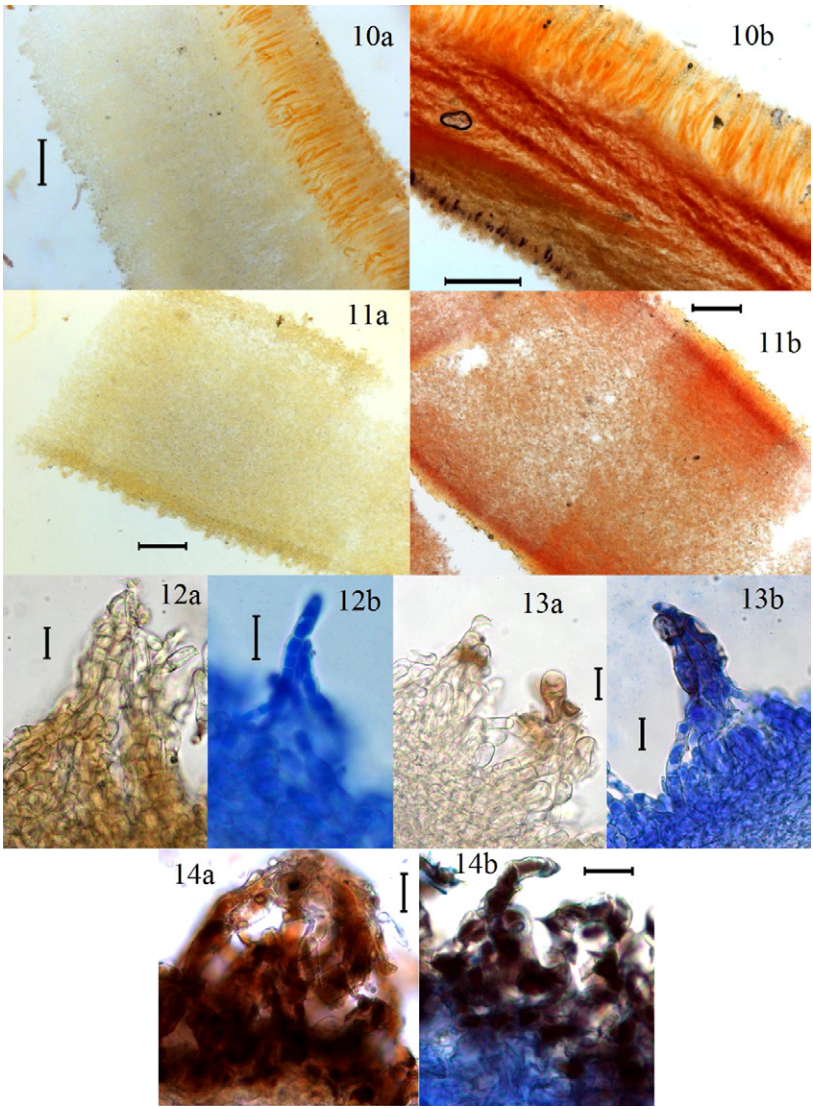
location, pigment may occur in the cytoplasm, in the wall, or encrusted on the wall (Figs 19–21). We observed that while the first two are constant within species, encrusted pigments are variable. For example, in *H. costifera* there are specimens with encrusted paraphyses and others without such incrustations. On the matter of pigment intensity, we return to cotton blue used first by Dissing (1964) to note that there are species where the cytoplasmic pigment color is so intense that it is still visible even after adding cotton blue, while others have lighter pigment no longer visible when adding the colorant (Figs 12–17). We realized that this characteristic is constant among specimens of the same species. This also happens with the pigment in the cell wall.

As indicated in the introduction, only Weber (1972, 1975) described the stipe tissue. We consider this character taxonomically valuable for the following reasons: 1) the hyphal fascicle lengths among specimens of the same species are more constant than in the apothecial sterile surface (see *H. hyperborea* remarks); 2) the pigments in the ectal excipulum and stipe outer layer can differ in water and cotton blue (see *H. ulvinenii* remarks; Fig. 22); and 3) the hemiamyloid reaction can occur in stipe tissue but not in the excipulum (e.g. *H. leucopus* var. *populina*).

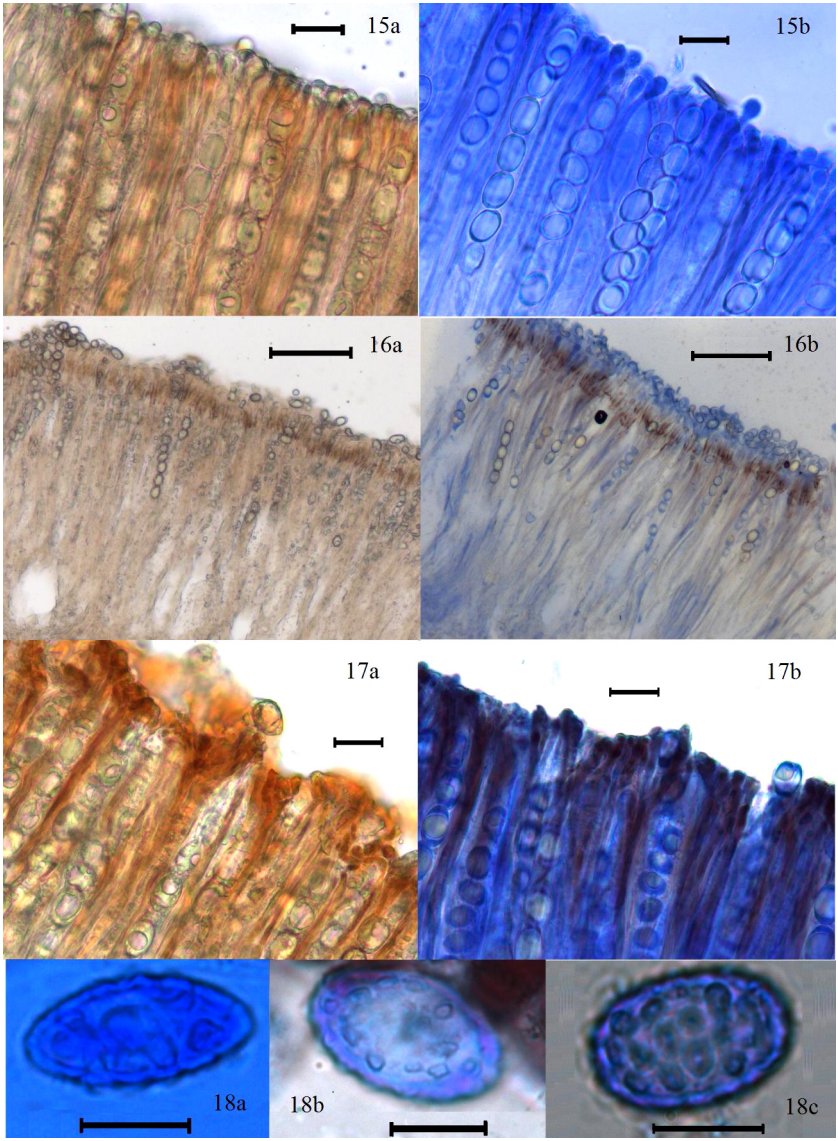
As Baral (1987) noted, we know little about hemiamyloid reaction, and there indeed are few records of this reaction in tissues other than the hymenium. We report this reaction in different apothecial and stipe tissues for *H. leucopus* var. *populina*, *H. robusta*, and *H. subglabra;* we have also observed this reaction in specimens of *H. albella* Quél., *H. connivens* Dissing & M. Lange (holotype), *H. elastica* Bull., and *H. stevensii* Peck (unpublished data).

Concerning ascospore ornamentation, we make the following points. 1) Ornamented ascospores are not restricted to *H.* subgen. *Macropodes* (here represented only by *H. macropus*, Fig. 18a) as Abbott & Currah (1997) proposed. We have also observed ornamented ascospores (generally only in mature ascospores outside the asci) in the type specimens of *H. leucopus* var. *populina* (Fig. 18b), *H. paraphysitorquata* (Fig. 18c), *H. solitaria, H. subglabra*, and *H. ulvinenii.* 2) We agree with Weber (1972) that it is the mature *Helvella* ascospores that are verrucose, contrary to the assumption of Dissing (1964) and Dissing & Nannfeldt (1966) that ornamented ascospores are the immature ones. 3) When citing ascospore sizes, it is important to indicate what kind of spores (smooth vs. ornamented) were measured, because in some species they have different size range (Fig. 9) (see remarks under *H. queletii*).

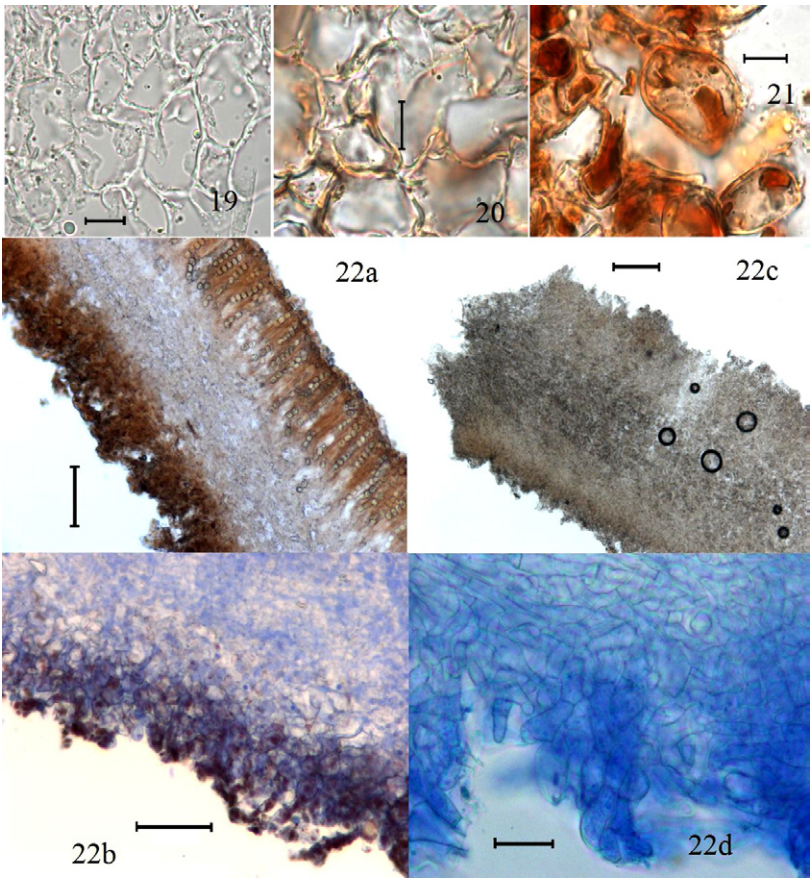
As noted previously, many different terms have been used to describe the apothecial and stipe outer layer surfaces, giving the impression that there were different types of hairs. However, in all cases these hairs are developmentally the same: they consist of hyphal clusters that differ only in length. The tiny hairs have been especially problematic; Weber (1972) and Abbott & Currah (1997)



Figs. 10–14. 10: Reaction of the apothecial excipulum to Melzer's reagent—a: negative (*Helvella solitaria*), b: hemiamyloid in medullary excipulum (*H. robusta*). 11: Reaction of stipe tissues to Melzer's reagent—a: negative (*H. hyperborea*), b: hemiamyloid in inner layer (*H. subglabra*). 12: Apothecium hyphal fascicles (*H. costifera*)—a: brown pigments visible in water, b) pigments not visible in cotton blue. 13: Apothecium hyphal fascicles (*H. griseoalba*)—a: only terminal cells are pigmented, b: pigments visible in cotton blue. 14: Apothecium hyphal fascicles (*H. dryadophila*)—a: brown pigments visible in water, b: brown pigments visible in cotton blue. Scale bars: 10a, 11a, 11b = 200 µm, 10b = 100 µm, 12–14 = 20 µm.



Figs. 15–18. 15: Paraphyses of *Helvella costifera*—a: brown pigments visible in water, b: pigments not visible under cotton blue. 16: Paraphyses of *H. paraphysitorquata*—a: brown pigments visible only in the thickened apices in water, b: pigments visible in cotton blue. 17: Paraphyses of *H. dryadophila*—a: brown pigments visible in water, b: pigments visible in cotton blue. 18: Ornamented ascospores in cotton blue—a: *H. macropus*, b: *H. leucopus* var. *populina*, c: *H. paraphysitorquata*. Scale bar: 15, 17 = 20 µm, 16a = 100 µm, 18 = 10 µm.



Figs. 19–22. 19: Hyaline ectal excipulum cells in water (*Helvella griseoalba*). 20: Wall pigments in ectal excipulum cells (*H. hyperborea*). 21: Wall and cytoplasmic pigments in ectal excipulum cells (*H. dryadophila*). 22: *H. ulvinenii*—a: apothecium thin section in water, b: ectal excipulum in cotton blue, notice the brown pigments, c: stipe layers in water, d: stipe outer layer under cotton blue. Scale bar: 19–21 = 10 µm, 22a, 22b = 100 µm, 22c = 200 µm, 22d = 20 µm.

used indistinct terms such as "finely pubescent," "furfuraceous," "granulose," or "granulose-roughened" — all with very different meaning. Here we propose to the term "subpubescent" to indicate that they have the same microscopic structure (i.e. are hyphal fascicles) of the hairs found on a "pubescent" surface but are simply shorter (Fig. 2). Likewise, longer hairs have been described as "pubescent" or "villose," without considering that the terms may refer to different types of hairs. We use "pubescent" (Fig. 3) to emphasize that *Helvella* has only one hair type that varies only in length. This agrees with Kaushal's (1991) terminology.

Reasons to retain *H. subglabra* as independent of *H. atra* and *H. griseoalba* separate from *H. costifera* are discussed below. We agree with Harmaja (1977a) that *H. queletii* is a synonym of *H. solitaria* and with Abbott & Currah (1997) that *H. dryadophila* is a synonym of *H. verruculosa*. We also propose *H. hyperborea* as a synonym of *H. costifera*.

We present below a synoptic key of the 12 *Helvella* species considered in this paper. Although not all *Helvella* species are included, we feel that this key provides additional morphological insights into the treated species and contributes to a better understanding of the genus.

Synoptic key to species of *Helvella* included in this work

1) *H. costifera* (= *H. hyperborea*)
2) *H. crassitunicata*
3) *H. griseoalba*
4) *H. leucopus* var. *populina*
5) *H. maculata*
6) *H. paraphysitorquata*
7) *H. pocillum*
8) *H. robusta*
9) *H. solitaria* (= *H. queletii*)
10) *H. subglabra*
11) *H. ulvinenii*
12) *H. verruculosa* (= *H. dryadophila*)

Apothecium shape (mature)
a. Cup-shaped 1, 2, 3, 7, 8, 9, 11, 12
b. Lobed 4, 5, 6, 8, 10

Apothecial sterile surface
a. Glabrous 2, 4
b. Subpubescent (hyphal fascicles < 50 µm long) 2, 7, 8, 9, 10, 11, 12
c. Pubescent, with hyphal fascicles 50–150 µm long 1, 3, 5, 6, 7, 8, 9, 11, 12
d. Pubescent, with hyphal fascicles > 150 µm long 1, 5, 6

Ribs (apothecial sterile surface)
a. Missing or reaching up to ¼ of the surface 2, 4, 6, 7, 9, 10, 11, 12
b. Reaching from ¼ to ¾ of the surface 1, 3
c. Reaching from ¾ to the edge of the apothecium 1, 5, 8
d. Simple 1, 5
e. Bifurcated 1, 3, 5, 8
f. Anastomosed 1, 8

Stipe (surface configuration)
a. Even 4, 10
b. Only ribbed 1, 2, 3, 7, 9, 11, 12
c. Ribbed and lacunose 5, 8
d. Consisting of 2–3 strands free or apically partly fused 6

Rib (stipe)
- a. Sharp-edged 5, 8
- b. Blunt-edged 1, 2, 3, 7, 9, 11, 12

Stipe (sterile surface)
- a. Glabrous 2, 3, 4
- b. Subpubescent (hyphal fascicles < 50 μm long) 2, 3, 8, 9, 10, 12
- c. Pubescent (hyphal fascicles 50–150 μm long) 1, 5, 6, 7, 8, 9, 11, 12

Stipe color
- a. Light tones 1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12
- b. Dark tones 4

Stipe context
- a. Solid 1, 2, 3, 6, 7, 9, 10, 11, 12
- b. Hollow 4, 5, 8

Ascus type
- a. Aporhynchous 2
- b. Pleurorhynchous 1, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12

Ascospore size
- a. Usually < 23 μm long 1, 3, 4, 5, 6, 8, 9, 10, 11, 12
- b. Usually > 23 μm long 2, 7

Thick-walled paraphyses
- a. Absent 1, 3, 4, 5, 7, 8, 9, 10, 11, 12
- b. Present 2
- c. Thickness restricted to the apex, forming a collar or hood 6

Melzer's reaction (medullary excipulum)
- a. Negative 1, 2, 3, 4, 5, 6, 7, 9, 11, 12
- b. Hemiamyloid (reddish) 8, 10

Meltzer's reaction (stipe inner layer)
- a. Negative 1, 2, 3, 5, 6, 7, 9, 11, 12
- b. Hemiamyloid (reddish) 4, 8, 10

Melzer's reaction (stipe outer layer)
- a. Negative 1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12
- b. Hemiamyloid (reddish) 8

Paraphyses (pigment topography)
- a. Absent 3
- b. In the cell wall 1, 7, 8, 10, 11
- c. In the cytoplasm 1, 2, 4, 5, 7, 9, 12
- d. Restricted to the apical collar or hood 6

Paraphyses (pigment in cotton blue)
- a. Not visible 1, 5, 8, 10
- b. Visible in all 2, 4, 7, 9, 11, 12
- c. Visible only in thickened apices 6

Pigment (ectal excipulum)
a. Absent 3, 4
b. In the cell wall 1, 2, 5, 6, 7, 8, 9, 10, 11, 12
c. In the cytoplasm 2, 5, 7, 9, 11, 12

Pigment (ectal excipulum in cotton blue)
a. Not visible 1, 5, 6, 8, 9, 10
b. Visible 2, 7, 11, 12

Pigment (stipe outer layer)
a. Absent 1, 3, 11
b. In the cell wall 2, 5, 6, 7, 8, 9, 10, 12
c. In the cytoplasm 2, 4, 5, 12

Pigment (stipe outer layer in cotton blue)
a. Not visible 2, 4, 6, 7, 8, 9, 10, 12
b. Visible in the cytoplasm 5

Pigment (apothecial hyphal fascicles)
a. Absent 5
b. In the cell wall 1, 2, 6, 8, 9, 10, 12
c. In the cytoplasm 2, 7, 11, 12
d. Restricted to the terminal cells (in the wall cell and cytoplasm) 3

Pigment (apothecial hyphal fascicles in cotton blue)
a. Not visible 1, 6, 8, 9, 10
b. Visible in the cytoplasm 7, 11, 12
c. Visible only in the cytoplasm in apical cells 3

Pigment (stipe hyphal fascicles)
a. Absent 1, 3, 5, 11
b. In the cell wall 2, 6, 7, 8, 9, 10, 12
c. In the cytoplasm 2, 12

Taxonomy of type specimens

Helvella costifera Nannf., in Lundell & Nannfeldt, Fungi Exsicc. Suec., Fasc. 41–42: 37, 1953 Figs 3, 12, 15, 23

≡ *Peziza costata* Fr., Nova Acta Reg. Soc. Sci. Uppsal., Ser. 3, 1: 120, 1851

Type: Sweden: Uppland, Uppsala, Botanic Garden, E.P. Fries s.n. *Peziza costata* (Lectotype UPS [not seen]; isolectotypes S [studied], K [not seen]).

= *Helvella hyperborea* Harmaja, Karstenia 18: 57, 1978

Asci 280–370 × 14–18 μm. Paraphyses 4.5–7.5 μm wide at the apex, thin-walled, hyaline, pale brown to brown in mass, pigment deposits in the cytoplasm and cell walls, few with brown pigment encrusted on the wall. Medullary excipulum hyaline to light brown. Ectal excipulum light brown, pigment deposits in the cell walls. Stipe inner and outer layers hyaline. Apothecial hyphal fascicles 100–230 μm long, light brown in mass, pigment deposits in the cell walls; stipe hyphal fascicles 50–120 μm long, hyaline. The brown

pigments of the ectal excipulum are not visible in cotton blue or Melzer's while those of the paraphysis cell walls are visible in Melzer's, but inconspicuous in cotton blue. All tissues rr–.

Additional specimens examined: **FINLAND**: **Lapland**, Enontekiö, 6 Aug 1985, J. Vauras 1932 (H); **Northern Ostrobothnia,** Kuusamo, 4 Aug 1994, T. Ulvinen FO23453 (OULU); **Uusimaa,** Lohja, 19 Jul 1998, U. Nummela-Salo & P. Salo 4924 (H). **NORWAY**: **Northern Norway,** Finnmark, 19 Aug 1995, I. Kylövuori 95-744 (H). **SWEDEN**: **Uppland**, 22 Jun 1948, H. Smith (UPS); 7 July 1948, A. Melderis (UPS); 9 Jul 1948, Exsiccata J.A. Nannfeldt no. 9956 (K).

Remarks — When Nannfeldt (Lundell & Nannfeldt 1953) transferred *Peziza costata* to *Helvella*, he had to publish a nom. nov., *H. costifera*, because the epithet "*costata*" was already occupied in *Helvella* by *H. costata* Schwein. In the protologue of the replaced synonym *Peziza costata*, Fries (1851: 120) had presented two syntypes:

"In Ohio Americae borealis (*Lindblom*) — etiam copiose in Horto Botanico Upsaliensi una cum *Pez. Helvelloidis* var. minori, *P. sepulta* (Cfr. Summ. Veg. Sc.) *Augusto* pluvio. *El. Fries*, filius [= Elias Petrus Fries]. … Descripti ad specimina Upsaliensia viva, a quibus exsiccatis Fungus Ohioensis non distinguendus."

Nannfeldt (1937: 64) noted that "*Peziza costata* Fr. is represented in the Uppsala Museum by beautiful authentical material," but Lundell & Nannfeldt (1953) cited none of Fries's specimens, noting only that the North American specimen cited by Fries is lost. Subsequently, a UPS syntype specimen collected by E.P. Fries was designated as **lectotype** by Dissing (1966b, as "holotype"), and accepted by Harmaja (1979, as "lectotype?") and Abbott & Currah (1997, as "holotype") — these errors in type terminology are correctable (McNeill et al. 2006: Art. 9.8).

The lectotype was not available for study because of the bad condition of the specimen at UPS. Dissing (1966b) described this species with narrower asci (12–15 µm) and paraphyses (3–4 µm) than we observed. Our isolectotype measurements are closer to those made by Abbott & Currah (1997; asci 313–381 × 13.3–17.1 µm, paraphyses 3.6–6.2 µm at the apex). *Helvella costifera* differs from *H. acetabulum* (L.) Quél. in being less ribbed, with blunt edged ribs, a non-lacunose stipe, grayish hymenium, and pubescent apothecium. In *H. acetabulum* the stipe is highly ribbed to lacunose with sharp edged ribs (Dissing 1966b), the hymenium has brownish tones (Weber 1972), and the sterile part of the apothecium is subpubescent to pubescent. See also discussion under *H. griseoalba* and *H. hyperborea*.

Helvella crassitunicata N.S. Weber, Beih. Nova Hedwigia 51: 30, 1975 Figs 5, 8, 24

Type: U.S.A.: Washington, Mount Rainier National Park, Narada Falls, on soil along a path, 10 Aug 1948, A.H. Smith 30052 (Holotype MICH, Barcode 11561).

Apothecium sterile surface subpubescent. Stipe glabrous to subpubescent. Asci 290–340 × 18–24 µm. Ascospores (21.5–)23–26(–28) × (12–)13–14.5 (–15.5) µm, ellipsoid to oblong, smooth. Paraphyses of two types: a) 5–7.5 µm wide at the apex, thin-walled, septate, hyaline or light brown; b) 7–9 µm wide at the apex, thick-walled, non-septate, light brown, pigment deposits always in the cytoplasm. Ectal excipulum brown, pigment deposits in the cell wall and cytoplasm. Stipe outer layer slightly lighter than the ectal excipulum of the apothecium, pigment deposits in the cell wall and cytoplasm. Apothecial hyphal fascicles ≤ 50 µm long, brown pigment deposits in cell walls and cytoplasm; stipe hyphal fascicles ≤ 10 µm long, tan pigment deposits in cell walls and cytoplasm. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible in cotton blue or Melzer's; light brown pigments of the stipe outer layer and hyphal fascicles inconspicuous in cotton blue or Melzer's. All tissues rr–.

Remarks — *Helvella crassitunicata* and *H. leucomelaena* (Pers.) Nannf. are the only two taxa with aporhynchous asci (Fig. 5) (Abbott & Currah 1997). *Helvella leucomelaena* is differentiated by mature paraphyses that are never thick-walled, slightly smaller (20–23(–25) × 10.5–14 µm) ascospores, and ascomata that fruit in spring or early summer. [However, although Weber (1972) cited *H. crassitunicata* as fruiting in the fall, Abbott & Currah (1997) noted it might fruit from May to October.] Also in *H. leucomelaena* the stipe is poorly developed or absent and the color of the paraphyses is lost in cotton blue.

Neither Weber (1972) nor we observed the following features cited for *H. crassitunicata* by Abbott & Currah (1997): 1) ectal excipulum "pubescent to densely pubescent", 2) stipe "finely pubescent to pubescent", and 3) asci 350–400 × 17–20 µm. It is uncertain whether the differences in wall thickness of the paraphyses should be interpreted as dimorphic (Abbott & Currah 1997) or developmental (young = thin-walled and mature = thick-walled; Weber 1975). Since a hymenium develops first as a palisade of paraphyses within which the asci develop, it would be difficult to have mature asci and immature paraphyses at the same time (Pfister pers. com.). On the other hand, we observed thin and thick-walled branches borne on the same paraphyses. See also remarks under *H. pocillum*.

Helvella dryadophila Harmaja, Karstenia 17: 58, 1977 Figs 14, 17, 21, 25

Type: NORWAY: prov. Oppland, par. Lom, fjled Høyrokampen, alt. 1400–1440 m, *Dryas octopetala* assoc., 29 Aug 1957 F.E. Eckblad, p.p. (Holotype O).

= ***Helvella verruculosa*** (Sacc.) Harmaja, Karstenia 18: 57, 1978

Asci 230–280 × 14–18 µm. Paraphyses 4–7 µm wide at the apex, thin-walled, brown, pigment deposits in the cytoplasm. Medullary excipulum hyaline. Ectal excipulum brown, pigment deposits in the cell wall and cytoplasm.

Stipe inner layer hyaline. Stipe outer layer brown, pigment deposits in cell wall and cytoplasm. Apothecial hyphal fascicles 40–100 µm, brown, pigment deposits in the cell wall and cytoplasm; stipe hyphal fascicles 30–70 µm, brown, pigment deposits in cell walls and cytoplasm. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible in cotton blue or Melzer's; brown pigments of the stipe outer layer and hyphal fascicles inconspicuous in cotton blue. All tissues rr–.

Remarks — We agree with Abbott & Currah (1997) that *H. dryadophila* is a synonym of *H. verruculosa*, because Harmaja (1977b, 1979) used variable characters to distinguish them. 1) Both ascomata appear the same: Harmaja's own illustration (1977b: 51) (Fig. 5) shows both species with a cup-shaped apothecium and a ribbed stipe with ribs that never reach the apothecial sterile surface. 2) For the excipulum, Harmaja cited, "the outermost layer has somewhat larger cells with slightly thicker wall as *H. arctoalpina,*" but gave no measurements, and we did not see such differences. 3) The paler and homogeneous contents of paraphyses in *H. dryadophila* did not appear paler to us; in fact, in cotton blue, the brown pigments are visible in the paraphyses of both species. The homogeneous content is variable and the pigment tends to be less homogeneous in immature ascomata. 4) As the presence of a fairly distinct layer of textura angularis in the excipulum is a generic character for *Helvella*, its occurrence should not be used to distinguish between species.

Abbott & Currah (1997) mentioned that *H. arctoalpina* Harmaja (Harmaja 1977) should also be considered a synonym of *H. verruculosa*, but as the type collection of *H. arctoalpina* is not in O, we unfortunately could not examine the holotype.

Helvella griseoalba N.S. Weber, Michigan Bot. 11: 162, 1972 Figs 2, 13, 19, 26

Type: U.S.A.: Michigan, Cheboygan Co., Grapevine Point, Douglas Lake, Univ. of Michigan Biol. Sta., 10 Jun 1968, N.J. Smith 982 (Holotype MICH, Barcode 14379).

Asci 220–265 × 12.5–16 µm. Medullary & ectal excipula hyaline. Stipe inner and outer layers hyaline. Apothecial hyphal fascicles 70–120 µm long, hyaline with brown terminal cells, pigment deposits in the cell wall and cytoplasm; stipe hyphal fascicles ≤ 30 µm long, completely hyaline. The brown pigments of terminal cells of the apothecial hyphal fascicles are visible in cotton blue or Melzer's. All tissues rr–.

Remarks — Although in fresh ascomata the hymenium and sterile surface of the apothecium are concolorous (gray to cinnamon; Weber 1972), the dried sterile surface is lighter, cream to light brown, and the hymenium is slightly darker, grayish brown. This may be one reason why dry *H. griseoalba* material can be easily confused with *H. costifera*. Both Häffner (1987) and Abbott & Currah (1997) synonymized *H. griseoalba* under *H. costifera,* noting that color

differences of the hymenial surface and absence of pigments in the apothecial ectal excipulum in *H. griseoalba* were not enough to separate them. However, we observed additional features in the types of *H. costifera* and *H. griseoalba* that support keeping them as different taxa: 1) *H. costifera* presents pubescent hyphal fascicles in the stipe while *H. griseoalba* does not (glabrous) or has shorter (subpubescent) hyphal fascicles; 2) *H. costifera* can have light brown paraphyses while *H. griseoalba* has only hyaline ones, and 3) in *H. griseoalba* the terminal cells of the apothecial hyphal fascicles have brown pigments that are visible in cotton blue (Fig. 13) while in *H. costifera* the light brown pigments in the cell walls are not visible in cotton blue (Fig. 12).

Helvella hyperborea Harmaja, Karstenia 18: 57, 1978 Figs 11a, 20, 27

Type: **FINLAND**: prov. Kuusamo, par. Kuusamo, Juuma, western part of the gorge Jäkälävuoma, alt. ca. 205 m, on a shady shelf in the basal part of a steep dolomitic rock, among the moss *Distichium capillaceum* (etc.), accompanied by *Salix reticulata, Saxifraga aizoides, S. nivalis, Woodsia glabella, Gerronema albidum*, 27 Aug 1970, H. Harmaja (Holotype H).

= ***Helvella costifera*** Nannf., in Lundell & Nannfeldt, Fungi Exsicc. Suec., Fasc. 41–42: 37, 1953

Asci 240–315 × 15–18 µm. Paraphyses thin-walled, hyaline, pale brown to brown in mass, pigment deposits in cytoplasm and cell walls, some with brown encrusted pigment on walls. Medullary excipulum hyaline to light brown. Stipe inner and outer layers hyaline. Apothecial hyphal fascicles 50–160 µm long, light brown in mass, pigment deposits in cell walls; stipe hyphal fascicles 50–100 µm long, hyaline. The brown pigments of all structures are not visible in cotton blue. All tissues rr–.

Additional specimens examined: **FINLAND**: **Lapland,** Kemi, 7 Aug 1998, U. Nummela-Salo & P. Salo 5318 (H); **Nortern Savonia**, Kuopio, 22 July 1984, J. Vauras 1638F (H); 23 Aug 1987, J. Vauras 2856 (H); **Varsinais-Suomen**, 4 Jul 1996, J. Vauras 11192F (H). **NORWAY**: **Northern Norway,** Troms, 16 Aug 1992, I. Kytövuori 92-352 (H).

Remarks — *Helvella hyperborea* was proposed as a new species by Harmaja (1978) and accepted as distinct by Abbott & Currah (1997). After comparing its type with *H. costifera,* including eleven additional specimens from Herbaria O and UPS (labeled either *H. costifera* or *H. hyperborea*), we conclude these two species are the same. Harmaja (1979, Table 1) listed 12 characters for differentiating *H. hyperborea* from *H. costifera* but explained that only a combination of all features should be used for its identification. In fact, we think that his table is an excellent presentation of variability in *H. costifera*. Abbott & Currah (1997) used only the ribs of the apothecial sterile surface to separate the species, distinguishing *H. costifera* by branched anastomosed ribs extending up to the marginal area from *H. hyperborea* with simple unbranched

ribs extending onto the basal half. However, both isolectotype and exsiccata (J.A. Nannfeldt no. 9956) of *H. costifera* possess the same features used to identify *H. hyperborea* (see Figs 23, 27).

We provide below our evaluation of what we consider the five most important features used by Harmaja (1979) to separate these species.

1) A brown-grey hymenium color that is paler in *H. costifera* — we have observed that in fresh material, the color intensity of the hymenium may depend on whether the specimen is growing in a forest clearing or in a shaded area.

2) Ribs extending onto the sterile surface, especially in dried specimens — Although Harmaja (1979; Figs. 2–3) illustrated this feature, we found that the *H. costifera* isolectotype also has ribs on the sterile surface as, for that matter, does *H. acetabulum*.

3) Sterile surface of the apothecium: "with fine but almost always ± distinct hyaline to pale brown pubescence or villosity" (*H. costifera*) versus "more or less delicate brown (mostly dark) pubescence usually appearing glabrous to bare eye" (*H. hyperborea*) — Under the microscope, the hairs of all studied specimens have the same color. However, we measured 100–230 µm long hyphal fascicles in the *H. costifera* type vs. 50–160 µm long fascicles in *H. hyperborea*. The hairs as measured in the additional specimens range from 50–240 µm long, depending on the maturity of the ascoma. In the stipe hair lengths are similar for both types — 50–120 µm long in *H. costifera*, 40–100 µm long in *H. hyperborea* — and remains relatively constant (40–120 µm) in the additional specimens.

4) Pigmentation of the paraphyses: "medium (rarely pale) brown wall encrustation" and more or less brown contents (*H. hyperborea*) versus hyaline, inconspicuous or pale brown encrustation and pale brown to practically hyaline contents (*H. costifera*) — We observed the same color in the paraphyses for both species, and in cotton blue the cytoplasmic pigment is inconspicuous; the cell wall pigment is variable among specimens in both species.

5) Distribution, "middle boreal to lower oroarctic (low alpine), optimal area apparently northern boreal zone" (*H. hyperborea*) versus "temperate to middle (oro)boreal with preference for southern and low-lying areas" (*H. costifera*) — Sequences of the 28s large subunit ribosomal DNA from three specimens identified as *H. costifera* (unpublished) from Scandinavia (two from northern boreal specimens and one from the middle boreal region) show only one or two base differences. Notably, both species were described from the Scandinavian peninsula.

Helvella leucopus* var. *populina I. Arroyo & Calonge, in Calonge, Bol. Soc. Micol. Madrid 25: 302, 2000 Figs 1, 18b, 28

Type: Spain: Guadalajara, Sigüenza, 8 May 1988, M.J. Rodríguez 888 (Holotype MA Fungus 22870).

Apothecium sterile surface glabrous, even. Stipe tapering toward the apex, hollow, glabrous. Asci pleurorhynchous. Ascospores verrucose, smooth within the ascus, hyaline, uniguttulate. Paraphyses 3.5–4.5 µm wide at the apex, thin-

walled, hyaline or brown, pigment deposits in the cytoplasm. Medullary and ectal excipula hyaline. Stipe inner layer hyaline. Stipe outer layer light brown, pigment deposits in the cytoplasm. Hyphal fascicles absent in the apothecium and stipe. The brown pigments of the paraphyses are visible and those of the stipe outer layer are not visible in cotton blue or Melzer's. Stipe inner layer rr+; medullary and ectal excipula and stipe outer layer rr–.

Remarks — Persoon (1822) described *H. leucopus* Pers. as having a deflexed apothecium at both ends (lobate), bay to black in color, and a 30–40 mm long glabrous white stipe. Arroyo & Calonge (1990) distinguished variety *populina* (validated by Calonge 2000) by the darker stipe color and larger ascoma size (apothecium 40–60 × 30–45 mm; stipe 50–120 × 15–35 mm). However, Moravec (1980) previously cited larger specimens of *H. leucopus* var. *leucopus* (ascomata ≤ 150 mm high) from Slovakia. Ascoma size can be quite variable and so should be considered with caution; for example, *H. crispa* (Scop.) Fr. and *H. lacunosa* ascomata may range from 50 to 200 mm high. Arroyo & Calonge (1990) described smooth ascospores and ≤ 12 µm wide paraphyses apices, while we observed verrucose mature ascospores (more evident in cotton blue or Melzer's) and narrower paraphyses.

Helvella maculata N.S. Weber, Beih. Nova Hedwigia 51: 27, 1975 Fig. 29

Type: U.S.A.: Idaho, Bonner Co., south side of Hoodoo Mountain, 5 Oct 1968, H.V. Smith et N.J. Smith (N.J. Smith 2124) (Holotype MICH, Barcode 5635).

Apothecium sterile surface pubescent. Ascospores 18–22.5 × 10.5–12 µm. Ectal excipulum yellowish brown, pigment deposits in cell walls and cytoplasm. Stipe inner layer hyaline. Stipe outer layer brown, pigment deposits in cell walls and cytoplasm. Apothecial hyphal fascicles 107–205 µm long, hyaline; stipe hyphal fascicles 60–130 µm long, hyaline. The brown pigments of the paraphyses and ectal excipulum of the apothecium are inconspicuous and those of the stipe outer layer are very conspicuous in cotton blue or Melzer's. All tissues rr–.

Remarks — We measured smaller ascospores than those cited by Weber (1975, 20–23 × 12–13.5 µm). *Helvella maculata* might be confused with *H. crispa*, but the mottled apothecium, grayish stipe ribs, pubescent sterile surface, and incurved and unrolling margin of *H. maculata* are diagnostic (Weber 1975; Abbott & Currah 1997). Furthermore, the brownish pigment of the stipe outer layer is evident in cotton blue in *H. maculata* but not in *H. crispa*. For Weber (1975) ascospore size could help differentiate the two species, but the size range we observed for *H. maculata* overlaps with that seen in *H. crispa* (16–20.5 × 9.8–12 µm). Another similar species, *H. fusca* Gillet, has a dark red-brown hymenium, distinctly ribbed sterile surface with some ribs reaching the apothecium margin, and vernal fructification associated with *Populus*,

Figs. 23–29: Ascomata of type specimens (except when indicated) of *Helvella*. 23: *H. costifera* (Exsiccata J.A. Nannfeldt no. 9956). 24: *H. crassitunicata*. 25: *H. dryadophila*. 26: *H. griseoalba*. 27: *H. hyperborea*. 28: *H. leucopus* var. *populina*. 29: *H. maculata*. Scale bar: 1 cm.

while *H. maculata* fruits in autumn and is associated with conifers (Weber 1975); furthermore, the apothecium sterile surface of *H. fusca* is subpubescent. According to Abbott & Currah (1997), *H. maculata* could also be confused with *H. lacunosa*, which differs in having an apothecium margin attached to the stipe, black hymenium, and glabrous sterile surface of apothecium and stipe.

Helvella paraphysitorquata I. Arroyo & Calonge, in Calonge & Arroyo, Mycotaxon 39: 210, 1990 Figs 7, 16, 18c, 30

Type: Spain: within the province of Teruel, Albarracín, growing in soil under *Populus*, 3 Jun 1988, I. Arroyo & F.D. Calonge (Holotype MA-Fungi 24512).

Apothecium sterile surface pubescent, even. Stipe pubescent. Asci pleurorhynchous. Ascospores 16.5–19 × 11–13.5 μm, ovoid to ellipsoid, verrucose, smooth within the ascus. Paraphyses 5–9 μm wide at the apex, thin-walled, hyaline, with a brown thick-walled cap or collar at the apex. Medullary excipulum hyaline. Ectal excipulum hyaline to light brown, pigment deposits in cell walls. Stipe inner and outer layers hyaline to light brown, pigment deposits in cell walls. Apothecial hyphal fascicles 60–220 μm long, hyaline to light brown in mass, pigment deposits in the cell wall; stipe hyphal fascicles 60–140 μm, hyaline to light brown in mass, pigment deposits in the cell wall. The brown pigments of the paraphyses are visible in cotton blue, and pigments of the ectal excipulum, apothecial hyphal fascicles, and stipe outer layer and hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr–.

Remarks — Calonge & Arroyo (1990) described *H. paraphysitorquata* with smooth ascospores, but we also found ornamented ascospores on the hymenial surface, stipe, and basal mycelium. We observed narrower paraphyses than those recorded by Calonge & Arroyo (1990; 7–10(–15) μm), possibly due to their rehydration in 2% KOH or 10% NH_3. *Helvella paraphysitorquata* is morphologically similar to *H. pezizoides* Afzel., which differs in its totally black even stipe and paraphyses lacking the brown collar. On the other hand, in a specimen determined as *H. macropus* from Mexico (J.M. Rodríguez Canseco 12, IBUG), we also observed a few or occasional brown capped or collared paraphyses, so apparently collared paraphyses are not unique to *H. paraphysitorquata*.

Helvella pocillum Harmaja, Karstenia 15: 30, 1976 Figs 4, 31

Type: Sweden: prov. Torne Lappmark, par. Jukkasjärvi, fjeld Låktatjåkko, on bare soil, 17 Aug 1946, L. Holm 472 (Holotype UPS).

Apothecium sterile surface subpubescent to pubescent, concolorous with the hymenial surface, stipe ribs only reaching the apothecium basis. Stipe 1–5 × 1–3 mm, solid, costate, ribs blunt, pubescent, concolorous with the hymenial surface. Asci 320–380 × 18–24 μm, pleurorhynchous. Ascospores 23–28 × 12–15.5 μm, smooth. Paraphyses thin-walled. Medullary excipulum hyaline. Ectal excipulum brown, pigment deposits in cytoplasm. Stipe inner layer hyaline. Stipe outer layer light brown, pigment deposits in cell walls. Apothecial hyphal fascicles 40–100 μm long, brown, pigment deposits in cytoplasm; stipe hyphal fascicles 50–80 μm, hyaline to light brown in mass,

pigment deposits in cell walls. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible and those of the stipe outer layer and hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr–.

Remarks — *Helvella pocillum* is characterized by its very small ascoma; only *H. rivularis* Dissing & Sivertsen is as small, but with an even stipe. For Harmaja (1976) *H. pocillum* could be separated from *H. crassitunicata* by its larger ascospores, the width of the paraphyses (we found no differences in either of these characters), and the absence of thick-walled paraphyses. Besides, *H. crassitunicata* has aporhynchous asci (Fig. 5) and the sterile surfaces of apothecium and stipe are glabrous to subpubescent. Another similar species is *H. leucomelaena*, also with aporhynchous asci.

Helvella queletii Bres., Fungi trident. 1(3): 39, 1882 Fig. 32

Type: Italy: Bosee di lance sopra Terzolaj, May 1882, J. Bresadola (Holotype S).

= ***Helvella solitaria*** P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 37, 1871

Stipe solid, costate, ribs blunt. Asci 260–310 × 15–20 µm, pleurorhynchous. Ascospores 17.5–21.5 × 10.5–12.5 µm, broadly ellipsoidal, smooth. Paraphyses 3.5–7 µm wide at the apex, thin-walled, brown, pigment deposits in the cytoplasm. Medullary excipulum hyaline. Ectal excipulum brown, pigment deposits in cell walls and cytoplasm. Stipe inner layer hyaline. Stipe outer layer light brown, pigment deposits in cell walls. Apothecial hyphal fascicles 25–60 µm long, light brown in mass, pigment deposits in the cell wall; stipe hyphal fascicles 40–100 µm, light brown, pigment deposits in cell walls. The brown pigments of the paraphyses are visible and pigments of the ectal excipulum, stipe outer layer, and apothecial and stipe hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr–.

Additional specimens examined: **SPAIN**: **Madrid**, Madrid, 7 Apr 2001, A. González, J.C. Campos et al., G.P. 1395 (MA-Fungi 73836); **Castile and León**, Valladolid, 31 Mar 2001, Herrera de Duero 1294 (MA Fungi 54822).

Remarks — Bresadola (1882), who described *H. queletii* as having a cup-shaped apothecium, sulcate-lacunose stipe ("costate" according to Weber 1972), and ascospores measuring 17–20 × 12 µm, noted its proximity to *H. lacunosa* but without mentioning the differences with *H. solitaria*. Dissing (1966b) differentiated *H. queletii* from *H. solitaria* by the following: 1) ascospore size — 17–19.1–21 × 11–12.3–13.5 µm (*H. queletii*) vs. 19–21.7–24 × 12–13.1–15 µm (*H. solitaria*); 2) ascoma size — 20–80 mm broad apothecium, 20–60 mm high stipe (*H. queletii*) vs. 10–40 mm broad apothecium, 10–25 mm high stipe (*H. solitaria*); 3) hymenium color (pale brownish to dark greyish-brown (*H. queletii*) vs. greyish to greyish-brown (*H. solitaria*); 4) stipe rib number — 4–7 in *H. queletii* vs. 2–5 in *H. solitaria*; 5) fruiting time — April–October in *H. queletii* vs. February–June in *H. solitaria*.

Harmaja (1977a) suggested that *H. queletii* be recognized as a synonym of *H. solitaria* based on the variability of ascoma size, color, pubescence, and stipe rib number. Abbott & Currah (1997) also considered them synonymous (but see below under *H. solitaria*). The following list summarizes our observations of both holotypes and other original descriptions.

1) The *H. solitaria* holotype has smooth ascospores and a spore range (18–20 × 9.5–12 μm) matching that of the *H. queletii* holotype and as reported by Dissing (1966b). We also found smaller (15–17.5 × 9.5–11.5 μm) verrucose ascospores more closely matching measurements given by Karsten (1871, 14–16 × 10 μm) but never matching that cited by Dissing (1966b).

2) Ascoma size, highly variable in *Helvella,* is not a good taxonomic criterion for a widespread species,

3) Ascoma color is highly variable in *H. queletii* with tones very similar to *H. solitaria,* as noted in Dissing (1966a) and Dissing & Nannfeldt (1966),

4) Among materials cited as *H. queletii* by Dissing (1966b) is a specimen collected in March (Velenovsky s.n., Mar 1923, PRC), while among his *H. solitaria* materials are specimens collected in July (Eftesøl s.n., 8 Jul 1956, O; Berg s.n., 15 Jul 1957, O), August (Bresadola s.n., Aug 1893, S; Hakelier s.n., 28 Aug 1962, UPS), September (P. Karsten s.n., 21 Sep 1866, H), October (Toft s.n., 21 Oct 1965, C), and November (Bresadola s.n., Nov 1896, S; Arwidsson s.n., 1 Nov 1943, S). Thus, the time of fruiting is not diagnostic.

5) Both holotypes are anatomically similar, except that the brown cytoplasmic pigment in the paraphyses is lighter in *H. solitaria*.

Helvella robusta S.P. Abbott, in Abbott & Currah, Mycotaxon 33: 242, 1988

Figs 10b, 33

Type: CANADA: Calgary, Nose Hill area, 30 Aug 1972, R.M. Danielson 459 (Holotype DAOM-143869).

Apothecium irregularly cupulate with a large central depression to irregularly bi-lobed, margin free, covering the stipe; sterile surface subpubescent to pubescent, ribbed, ribs sharp. Stipe gradually expanding toward the apothecium, lacunose, ribs sharp, subpubescent to pubescent. Paraphyses hyaline to light brown, pigment deposits in cell walls. Medullary excipulum hyaline. Ectal excipulum light brown, pigment deposits in cell walls. Stipe inner layer hyaline. Stipe outer layer light brown, pigment deposits in cell walls. Apothecial hyphal fascicles 38–80 μm long, hyaline to light brown, pigment deposits in cell walls; stipe hyphal fascicles 40–90 μm long, hyaline to light brown, pigment deposits in cell walls. The brown pigment of the paraphyses, ectal excipulum, apothecial hyphal fascicles, and stipe outer layer is not visible in cotton blue or Melzer's. Medullary excipulum and stipe inner and outer layers rr+; ectal excipulum rr–.

Remarks — Abbott & Currah (1988, 1997) described *H. robusta* with apothecium that is irregularly cupulate or centrally depressed with reflexed margins; in addition to this type, we observed an irregularly bi-lobed apothecium covering the stipe, with the apothecial edges curved towards the stipe, thus fully exposing the hymenium. The peculiar shape of the ascoma makes *H. robusta* easy to recognize, although Abbott & Currah (1988) noted that it could be confused with some species of section *Acetabulum*, although members of that section have a well-defined cup-shaped apothecium in all stages of development. In addition to its peculiar apothecial shape, *H. robusta* has a strong reddish reaction in the apothecial medullary excipulum and stipe inner layer and moderately reddish reaction in the stipe outer layer in Melzer's.

Helvella solitaria P. Karst., Bidr. Känn. Finl. Nat. Folk 19: 37, 1871 Figs 9, 10a, 34

Type: Finland: Mustiala, in horto, ad marg. rivula, 21 Sep 1866, P. Karsten PAK 3288 (Holotype H).

= *Helvella queletii* Bres., Fungi trident. 1(3): 39, 1883

Ascospores a) smooth: 18–20 × 9.5–12 µm, broadly ellipsoidal; b) verrucose: 15–17.5 × 9.5–11.5 µm, ellipsoidal. Paraphyses 4–7 µm wide at the apex, thin-walled, light brown, pigment deposits in the cytoplasm. Medullary excipulum hyaline. Ectal excipulum brown, pigment deposits in cell walls and cytoplasm. Stipe inner layer hyaline. Stipe outer layer light brown, pigment deposits in cell walls. Apothecial hyphal fascicles 40–90 µm long, light brown, pigment deposits in cell walls; stipe hyphal fascicles 35–90 µm, light brown in mass, pigment deposits in cell walls. The brown pigments of the paraphyses are visible, and pigments of the ectal excipulum, stipe outer layer, and apothecial and stipe hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr–.

Remarks — *Helvella solitaria* can be confused with *H. pocillum*, *H. ulvinenii,* and *H. verruculosa* because of its cup-shaped apothecium, costate stipe with ribs extending only to the base or a short distance onto the apothecium, and pleurorhynchous asci. *Helvella pocillum* has larger ascospores (22–30 × 13–17 µm). *Helvella ulvinenii* has brown, sepia to black apothecial sterile surface (never with grayish tones), brown pigment of the apothecial hyphal fascicles visible in cotton blue and hyaline stipe hyphal fascicles. *Helvella verruculosa* differs in the visibility of the brown cytoplasmic pigments in the ectal excipulum and apothecial hyphal fascicles in cotton blue, and its arctic and alpine distribution contrasts with the boreal and temperate distribution for *H. solitaria* (Abbott & Currah 1997).

Paraphysis widths cited here match those by Karsten (1871) but not those by Abbott & Currah (1997), who cited paraphyses with 7–8 µm wide apices. Karsten (1871) gave 14–16 × 10 µm for *H. solitaria* ascospores but did not

mention whether they were smooth or ornamented. We agree with Harmaja (1977a,b) that mature and immature ascospore sizes differ in some species, but in view of the greater size variation in *H. solitaria*, we consider it important to list the sizes of both immature and mature ascospores.

Although Dissing (1966b) recognized *H. solitaria* and *H. queletii* as different species, we agree with Harmaja (1977a) that they are synonyms, with the name *H. solitaria* having priority (see discussion under *H. queletii*).

According to Abbott & Currah (1997), *H. solitaria* sensu Dissing (1966b) corresponds to *H. leucomelaena*. We do not agree with this because of the following: 1) *H. leucomelaena* has aporhynchous asci; Dissing (1966b) did not mention the ascus base, and 2) the specimens studied by Dissing do not seem to correspond to a single species. Harmaja (1977a) designated one Dissing *H. solitaria* specimen as holotype of *H. confusa* Harmaja (also considered a synonym under *H. leucomelaena* by Abbott & Currah, 1997), while other Dissing specimens correspond to different species, among them *H. leucomelaena* and *H. solitaria* (Harmaja 1979). As Dissing's concept of *H. solitaria* was very broad, it cannot be attributed to a particular taxon.

Helvella subglabra N.S. Weber, Michigan Bot. 11: 179, 1972 FIGS 6, 11b, 35

TYPE: U.S.A.: Michigan, Washtenaw, Co., Stinchfield Woods, near Dexter, 13 Oct 1968, N.J. Smith 2145 (Holotype MICH, Barcode 14381).

ASCI 224–324 × 15–17 µm, pleurorhynchous. ASCOSPORES 15–19 × 10–11.5 µm, smooth, few verrucose. PARAPHYSES thin-walled, hyaline to pale brown, pigment deposits in the cell wall. STIPE OUTER LAYER brown, pigment deposits in the cell wall. APOTHECIAL & STIPE HYPHAL FASCICLES ≤ 30 µm long, scattered; hyaline to brown, pigment deposits in cell walls. The brown pigments of all structures are not visible in cotton blue. Medullary excipulum and stipe inner layer rr+; ectal excipulum and stipe outer layer rr–.

REMARKS — Häffner (1987) and Abbott & Currah (1997) synonymized *H. subglabra* under *H. atra* J. König. They considered that the differences listed by Weber (1972) were not enough to separate them, because other species (*H. lacunosa*, *H. albella*, *H. latispora* Boud.) also accommodate such variability. Distinctions noted by Weber (1972) are: 1) hymenium surface color— dark gray to brownish gray or drab (*H. subglabra*) vs. black to grayish black (*H. atra*); 2) color of stipe and apothecial sterile surface — drab to gray (*H. subglabra*) vs. black or dark gray (*H. atra*); 3) pigments in cells of the ectal excipulum — scattered hyphal cells with brown walls (*H. subglabra*) vs. most hyphal cells with brown walls (*H. atra*); and 4) apothecial sterile surface texture — subpubescent (*H. subglabra*) vs. completely glabrous (*H. atra*). We add here two more characters that separate *H. subglabra* from *H. atra*: 1) tissues in Melzer's — ascoma negative (*H. atra*) vs. apothecial medullary excipulum

Figs. 30–37: Ascomata of type material of *Helvella*. 30: *H. paraphysitorquata*. 31: *H. pocillum*. 32: *H. queletii*. 33: *H. robusta*. 34: *H. solitaria* (scanned image of the picture contained in the type specimen). 35: *H. subglabra*. 36: *H. ulvinenii*. 37: *H. verruculosa*. Scale bar: 1 cm.

weakly reddish and stipe inner layer strongly reddish (*H. subglabra*); 2) the brown cell wall pigment in the paraphyses, ectal excipulum, and stipe outer layer is visible in cotton blue in *H. atra*.

Helvella ulvinenii Harmaja, Karstenia 19: 42, 1979 Figs 22, 36

Type: Finland: prv. Enontekiön Lappi, par. Enontekiö, Kilpisjärvi, NE slope of W peak of fjeld Pikku-Malla, alt. ca. 650 m, H. Harmaja, 25 Aug 1979 (Holotype H).

Apothecium sterile surface subpubescent to pubescent. Stipe solid, costate, ribs blunt, pubescent. Asci 240–300 × 14–17 µm. Ascospores 14.5–18.5 × 10.5–12(–13.5) µm, broadly ellipsoid, smooth and verrucose. Stipe inner & outer layers hyaline. Apothecial hyphal fascicles 40–105 µm long, brown, pigment deposits in the cytoplasm; stipe hyphal fascicles 60–140 µm, hyaline. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible in cotton blue or Melzer's. All tissues rr–.

Remarks — Harmaja (1979) did not mention ascospore ornamentation for *H. ulvinenii*; we observed both smooth (immature), and verrucose (mature) ascospores with the same size and shape. *Helvella ulvinenii* shares cup-shaped apothecia and costate stipes with ribs that do not reach the sterile apothecial surface with *H. solitaria* and *H. verruculosa*. We agree with Harmaja (1979) that *H. ulvinenii* is distinguished from *H. solitaria* by 1) a darker sterile surface that is never grayish, 2) shorter ascospores, and 3) ectal excipular hyphae with distinctly dark pigments, present only in the cell wall and not in the cytoplasm. Additional distinctions include: 1) the stipe outer layer and hyphal fascicles are hyaline in *H. ulvinenii* and light brownish (on the cell walls) in *H. solitaria*, and 2) the apothecial hyphal fascicle pigments are deposited in the wall in *H. solitaria* and occur both in the cytoplasm and in the cell wall in *H. ulvinenii*.

Harmaja (1979) differentiated *H. verruculosa* (as *H. dryadophila*) from *H. ulvinenii* based on 1) apothecial shape, 2) longer ascospores, and 3) very long paraphysis end cells. Although we did measure longer ascospores (17.5–22 × 10.5–13 µm) for *H. verruculosa*, both types had cup-shaped apothecia and ribbed stipes and the paraphysis end cells appeared the same. In addition, we observed that *H. verruculosa* has pigmented stipe hyphal fascicles. Probably, *H. ulvinenii* is a variety of *H. verruculosa*.

The *H. ulvinenii* type demonstrates particularly well the differences between the structure of the ectal excipulum and apothecial hyphal fascicles and of the stipe outer layer and hyphal fascicles; cells are pigmented in the apothecium and hyaline in the stipe (Fig. 22).

Helvella verruculosa (Sacc.) Harmaja, Karstenia 18: 57, 1978 Fig. 37

Type: Russia: Madagan Obl., Chukotski Peninsula, Arakamchene Island by the Bearing Strait, Stony Hills, 11 Aug ca. 1885, Wright, Herb. U.S.N. Pacif. Expl. Exped. No. 369 (Holotype K, Isotype FH, both studied).

= *Geopyxis verruculosa* Sacc., Sylloge fungorum 8: 68, 1889

= *Helvella dryadophila* Harmaja, Karstenia 17: 58, 1977

Paraphyses 4–8 µm wide at the apex, thin-walled, brown, pigment deposits in the cytoplasm. Medullary excipulum hyaline. Ectal excipulum brown, pigment deposits in cell walls and cytoplasm. Stipe inner layer hyaline.

Stipe outer layer brown, pigment deposits in cell walls and cytoplasm. Apothecial hyphal fascicles 70–150 µm, brown, pigment deposits in cell walls and cytoplasm; stipe hyphal fascicles 50–130 µm, brown, pigment deposits in cell walls and cytoplasm. The brown pigments of the paraphyses, ectal excipulum, and apothecial hyphal fascicles are visible and those of the stipe outer layer and hyphal fascicles are not visible in cotton blue or Melzer's. All tissues rr–.

Remarks — Abbott & Currah (1997) described this species with a "villose margin" of the apothecium (sometimes with distinct white hairs), the stipe as having few chambers, and with stipe ribs extending onto basal half of apothecial sterile surface. We did not observe the marginal hairs, perhaps because the hairs have been lost due to age or handling. Furthermore, we observed neither stipe chambers nor ribs on the sterile surface of the apothecium. In fact, *H. verruculosa* is more easily confused with *H. solitaria* and *H. ulvinenii*, which do not have ribs on the sterile surface (see differences under the remarks of these species) than with *H. acetabulum*, *H. costifera*, and *H. griseoalba*.

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